Phenotypical Differentiation of Endemic Birds in Relation to Island Size in Micronesia

Yoshimaro YAMASHINA

Introduction

Students of evolution are well aware of the important role of islands in the development of living organisms. However, so far as birds are concerned, most investigators have dealt chiefly with the relation between richness of the avifauna and the ecological conditions of the island supporting it. Rarely have they been concerned with the relation between the amount of phenotypical differentiation on each island and the environmental conditions, past or present, of the island on which it developed. Lack in his studies on the Darwin's Finches of the Galapagos Islands (1947) states his belief that the effects of isolation and adaptation are the most important factors influencing speciation of birds in those islands, and admits the effects of accidental elimination and recombination of hereditary characters suggested by Wright (1940) only in a few cases of subspeciation. My recent studies on Micronesian birds suggest the existence and effectiveness of such non-adaptive differentiation factors not only in the development of subspecies, but also in the formation of species and genera. The evidence leading to this conclusion follows:

The following Micronesian islands contain endemic land birds:

North Mariana Islands: Assongson, Agrigan, Pagan, and Almagan.
South Mariana Islands: Saipan, Tinian, Agiguan, Rota, and Guam.
Palau Islands: Babelthuap, Koror, Peiliiu, Angaur, Pulo Anna, etc.
Marshall Islands: Jaluit, Iringiöb, Arhno, Wotze, and Bikini.

About 38 endemic species and 5 endemic genera live in these islands (cf. Handlist of Japanese Birds, 3rd ed., 1942; Mayr 1945).

These islands may be classified into five types, based on their origin and probable age as follows:

I. Coral Islands.
II. Islands formed by extrusion of Andesite in the Pleistocene and Holocene.
III. Islands of Pleistocene emergence.
IV. Islands of probable Pliocene emergence.
V. Islands formed by extrusion in the early Tertiary.

1) I am highly indebted to Professor Risaburo Tayama of Tohoku University for supplying the accompanying geological data on the Micronesian Islands.
I. Coral Islands:

Coral islands, formed only of coral reefs, are found in the western Caroline and the Marshall groups. The wide spread species, *Acrocephalus luscinia* is met with in Wolea, Lamotrek, Lukunor, and Nukuoro in the Carolines and *Ducula oceanica* occurs in the Marshalls. Except for *Ducula oceanica ratakensis* in the Ratak chain, they do not vary even subspecifically, indicating quite recent tenure of their present habitats.

II. Islands formed by Extrusion of Andesite in the Pleistocene and Holocene:

The North Mariana Islands were formed by extrusions of Andesite from the Pleistocene onward. Some of these islands are still active volcanos. The following six land-birds have been captured in these volcanic islands.

- *Gallinula chloropus*: Pagan.

All these species are widely distributed throughout the Marianas, or the whole of Micronesia, and only two species, *Acrocephalus luscina* (yamashinai) and *Halcyon chloris* (owstoni) differ subspecifically from those of the South Marianas. Therefore, these land-birds must have appeared fairly recently in these newly formed volcanic islands.

III. Islands of Pleistocene emergence.

Rota and Tinian in the South Marianas are said to have originated by submarine volcanic action during the Miocene, and to have emerged above the sea surface in the Pleistocene after coral-limestone deposition during the Pliocene. Rota emerged later than Tinian. Tinian has 13 land birds and Rota
11. All except one species in Tinian, *Monarcha takatsukasae*, are distributed throughout the whole Marianas. This fact indicates that the island is too new to have formed a number of new species or races.

The one unique endemic bird in Tinian island deserves further comment. *Monarcha takatsukasae* is a most interesting species from the evolutionary point of view. It is one of the slender-billed Broadbills, showing characteristics of *Monarcha*, but if the adult plumages alone are compared, without near relatives in the neighboring islands. However, the plumage color and body structure of this bird show remarkable similarities to the juvenile of the Yap Broadbill, *Monarcha godeffroyii*. The only differences between them are slightly larger size and duller color of plumage in the latter. Combining this fact with the geological history of the island indicates that *Monarcha godeffroyii* must be the ancestor of *Monarcha takatsukasae*. *M. godeffroyii* probably came to Tinian when the island was still very small, immediately after its emergences above the sea surface. The ancestor of the *Monarcha takatsukasae* must have had a very small population at some geological period, and atavistic mutation and dimidiation probably produced the new species despite the youth of the island.

IV. Islands of Probable Pliocene emergences.

Truk, Kusaie, and Guam are said to be similar in age. The basic strata of these islands are said to be pre-Miocene rock, basalt in the two former, andesite in the last. These islands appeared above the sea-surface in the Pliocene, and are rather old compared with the islands mentioned previously. Each island has a number of endemic birds as follows:

**Truk Island:**
- *Kubaryum ruki*<sup>2)</sup>
- *Myiagra oceanica*
- *Metabolus rugensis* (Muscicapidae)

**Kusaie Island:**
- *Aplonis corvina*
- *Aphanolimnas monasa* (Rallidae)

**Guam Island:**
- *Myiagra freycineti*
- *Rallus owstoni*

Such species as *Corvus kubaryi*, and *Ptilinopus roseicapillus*, which are not endemic to Guam, but to the whole South Marianas, might have been formed in Guam.

<sup>2)</sup> Mayr (1944) selected *Rukia* Momiyama, *Birds of Micronesia*, p. 2 (1922) for this genus, but *Kubaryum* Momiyama, *loc. cit.* p. 1 (1933) has page priority over *Rukia*, and must be used instead.
Here we must notice that single monotypic genera exist respectively on Truk (Metabolus) and Kusaie (Aphanolimnas), but none on Guam. This phenomenon may be explained as follows. These three islands are similar in age as mentioned above, but the shape of the mountain forming the islands is different. Truk and Kusaie are formed by single cone-type volcanos having very slender summits and steep slopes. Thus the area of the islands must have been very small especially in their period of submergence, though the peak of the island, at least, is believed to have been always above the sea. The ancestor of Metabolus, which might have been of Monarcha stock, and that of Aphanolymnas, which was perhaps related to Porzana tabuensis, probably came from somewhere in the Melanesian Islands and survived in these very small islands in very small populations. Under such circumstances a peculiar type could easily have developed. On the other hand, Guam was not originally a single cone-type volcano, and its area therefore was never as small as Truk and Kusaie once were, even at its period of extreme submergence. Race-formation by the spreading of mutant genes was discouraged in Guam by the larger population it supported. Therefore no monotypic genus, characterized by extreme morphological differentiation, was formed on Guam despite its similarity in age and origin to Truk and Kusaie.

V. Islands Formed by Extrusion in the Early Tertiary.

Saipan, Yap, Palau, and Ponape are said to be islands of this type. They are the oldest and largest of the Micronesian islands. The endemic species of birds found in these islands are as follows:

Saipan: Cleptornis marchei.
Yap: Kubaryum oleaginea, Edolisoma nesiotes, Monarcha godeffroyi.
Palau: Kubaryum palauensis, Zosterops finschi, Colluricincla tenebrosus,
Lalage monacha, Psamathia annae, Otus podargina, Gallicolumba canifrons.

Ponape: Aplonis pelzelni, Kubaryum longirostra, Lalage insperata, Trichoglossus rubiginosus.

Among these endemic birds we find only two monotypic genera, Cleptornis marchei (Meliphagidae) and Psamathia annae (Sylviidae) in Saipan and Palau respectively. This apparent anomaly may be explained by the geological history of each island. Ponape and Yap are believed always to have been large in area. Ponape was originally a homate-type volcano, with a very wide flat summit. Therefore, the land area of the island was apparently large, even when the island was in extreme submergence. The geological origin of Yap is peculiarly unique. The basic stratum of this island is Amphibolite, which is usually found on continents, not in oceanic islands. Some investigators therefore consider this island to be a remnant of a lost continent. The hypothesis is very doubtful, but it is generally accepted that the size of the island has been larger in the geological past than today. Thus the population of immigrant birds in these two islands probably were not small enough over a long enough period to allow for strong differentiation to develop. Therefore, Ponape and Yap have no monotypic genera, though they have several endemic species. On the other hand,}

3) Mayr (1933, 1944, 1945) insists on the validity of the name Rhamphozosterops sanfordi Mayr for this bird, basing his claim erroneously on priority of publication. Cinnyrorhyncha longirostra Takatsukasa and Yamashina was described in vol 43, no. 516 of Dobutsugaku Zasshi dated 15 Oct. 1931, and mailed 19 Oct. 1931, at least 16 days before the description of R. sanfordi Mayr was published. Mayr (1944, 8) refutes this date, claiming the description of C. longirostra was not published until 23 Nov. 1931, a fact he ascertained "by correspondence with leading American and European ornithologists and libraries". The date he mentions, 23 Nov. 1931, is the publication date of Vol. 43, No. 517 of Dob. Zasshi. All members of the Zoological Society of Japan residing in Tokyo received No. 516, containing the mooted description, between 20 and 25 October, as verified by the library records of the Yamashina and Kuroda libraries (the last was unfortunately destroyed during the war) and by the Momiyama diary, fortunately still extant, which shows this particular number reached his residence in Sasazuka, near Tokyo, 24 Oct. 1931. Therefore, according to the International Code of Nomenclature, C. longirostra Takatsukasa and Yamashina has priority over R. sanfordi Mayr, and must be accepted as valid.

I consider Cinnyrorhyncha, Megazosterops and Kubaryum to be congeneric.

Fig. 3. Otus (Pyrroglaux) podargina captured in Babelthuap Island, the Palau Islands, and kept in the author's aviary in Tokyo. Photographed by Y. Yamashina, August 1938.
Saipan was a cone-type volcano with a very narrow summit similar to those of the North Marianas. In the time of its extreme submergence, only a very narrow peak, now called Mt. Sankaku, appeared above the sea-surface. The entire island, except Mt. Sankaku, is covered with tertiary coral-limestone. In Palau Island where the highest peak is only 240 meters above the sea, the tertiary coral-limestone covers about 200 meters above the sea surface. Thus only 40 meters of summit was above the sea surface when Palau was in extreme submergence. Conditions in Saipan and Palau were, therefore, quite similar to those in Truk and Kusaie and the small ancestral populations of Cleptornis and Psamathia could similarly have differentiated strongly in these small solitary, well isolated islands.

Discussion and Conclusions

All the Micronesian islands are of volcano origin, extruded independently from an underwater ridge on the bottom of the Southwest Pacific ocean. There is no evidence of any land-bridge having existed either between each island or between the islands and neighboring lands. That is to say, all Micronesian Islands are purely oceanic.

We must consider therefore that all land-birds living in these islands have immigrated of their own accord from neighboring land areas, excepting those few species which were imported by man.

Some species of birds, generally regarded as resident and non-migratory, sometimes appear to make sudden long journeys. In the Bonin Islands Corvus coronoides japonensis was once a resident, but was extirpated before 1920. A flock of about 17-18 Corvus corone orientalis suddenly appeared in the islands in November, 1933 (Yamashina 1934), and was totally destroyed by hunters within a year. This shows, however, that birds which are usually sedentary, may migrate to remote oceanic islands.
Phenotypical differentiation after birds have immigrated to an island is affected by the degree of isolation, the frequency of gene mutation, the number of generations, the size of population, and the degree of selection. Here in the oceanic islands, the isolation is complete. The frequency of gene mutation has no apparent relation to size of islands or populations. They have been sufficient to produce varying degrees of phenotypical differentiation in the birds living on every island in question. Therefore, the other three factors, number of generations, size of population, and degree of selection must be the major determinants.

All the islands supporting monotypic endemic genera were once very small in area. Namely, Palau and Saipan among the older islands and Truk and Kusaie among the newer, possess endemic monotypic genera equally, while older Yap and Ponape, which have always been larger have only endemic species. Among the comparatively newer islands, only Tinian, which once was very small, has an endemic species. These facts suggest that the smallness of the size of population must be an important factor in the phenotypical differentiation of birds in oceanic islands.

Hardy (1908) and Wright (1921, 1940) have proved statistically that race formation is advanced without selection in a certain direction, if the frequency of gene mutation is sufficient. These observations in the Micronesian islands, while endorsing Hardy’s and Wright’s theory to some extent, suggest that smallness of populations is more important than length of tenure and natural selection in the evolution of animals in isolated oceanic islands.

**Literature Cited**


Mayr, E. 1933. Ibis, p. 389


1936. Topography, Geology, and Coral Reef of Tinian Island.

1936. Topography, Geology, and Coral Reef of Ponape Island.

1938. Topography, Geology, and Coral Reef of Saipan Island.


